

WILDLIFE BIOLOGY

Short communication

Using high-density SNP genotyping to determine the origin of wild boar dispersers outside the geographic range margins in Norway

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Mammalian dispersal is characterized by long-distance movements, and whether dispersal is sex-dependent and occurs at pre-saturation densities affects colonization speed and concurrent pathogen spread. In Scandinavia, Sweden classifies wild boar *Sus scrofa* as a native species and retains high densities, while Norwegian authorities consider it an alien invasive species and maintains the population at a minimum. With a long shared border and the recent detection of African swine fever (ASF) in Sweden, long-distance dispersal of wild boar into Norway is a concern. Using high-density single nucleotide polymorphism (SNP) analysis of relatedness among 192 wild boar distributed across Sweden and Norway, we report sex and determined the likely origin of seven dispersing individuals detected far outside of the current Norwegian range margins. Dispersal distances varied from 61 to 431 km (mean = 230) and all seven dispersers were males, which reduces the likelihood of successful reproduction and establishment. Five of the wild boar originated from the low-density population at the colonization border in Norway, indicating pre-saturation dispersal. Sweden is of interest given the risk of pathogen spread. However, in the current epidemiological situation, we nevertheless consider it very unlikely that ASF will enter Norway by long-distance wild boar dispersal.

Keywords: African swine fever (ASF), dispersal, sex, SNPs, *Sus scrofa*, wild boar



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Introduction

Mammalian dispersal is characterized by long-distance movements (Bowler and Benton 2005), and whether dispersal is sex- and density-dependent affects gene flow, colonization speed, concurrent pathogen spread and a range of other processes. Pre-saturation dispersal, i.e. dispersal from an area that has not reached its carrying capacity, favours rapid colonization, while male-biased dispersal limits establishment (Swenson et al. 1998). The dispersal process consists of emigration, transfer and immigration. Patterns of dispersal are therefore typically context-dependent (Aars and Ims 2000), and emigration and immigration processes may differ between endemic areas compared to range margins.

Management of wild boar *Sus scrofa* in Europe is topical due to their invasive potential (Sales et al. 2017), challenges in controlling the species (Massei et al. 2015) and the ongoing spread of African swine fever (ASF; Dellicour et al. 2020). However, we know little about wild boar dispersal at the northern colonization front in Europe. In Scandinavia, wild boar were extirpated, and the current transboundary populations were founded by escaped wild boar during the 1980s in Sweden. Norway and Sweden share a 1630 km long and largely unfenced border, across which the management aims differ. Wild boar are considered an alien, invasive species in Norway, but a native species in Sweden (The Swedish Environmental Protection Agency 2020).

The annual number of harvested wild boar has grown to > 100 000 in Sweden but remains < 500 in Norway, partly due to differing management policies. Alongside growing populations, there has been an increase in observations of long-distance dispersers more than 300 km outside the current geographic range margins in Norway. The first and only recorded outbreak of ASF in Sweden was in 2023 (Chenais et al. 2024), and has raised questions about whether these long-distance dispersers in Norway originate from 1) the much larger Swedish population, and/or 2) the low density colonization front in Norway. Wild boar are now established and self-sustaining also in Norway, so genetic relatedness analysis can aid to differentiate between the two possibilities.

We report sex and body weight of all dispersing wild boar detected far outside of the current distribution range margins in Norway. To trace their likely origin, we generated

relatedness assignments covering the main distribution range of wild boar in Norway and Sweden.

Material and methods

A total of 192 tissue samples from wild boar were obtained through either legal hunting in Norway (2019–2021; n=126) or from wild boar found dead or killed in traffic accidents in Sweden (1994–2021; n=66). The samples covered the distribution range in Norway and Sweden, including all seven dispersers known to be shot outside of the main geographic range margins in Norway (Table 1). All wild boar observed outside of the main distribution range were shot irrespective of sex or age, and all were genotyped.

Genomic DNA was extracted using the Qiagen DNeasy 96 Blood and Tissue Kit (Qiagen, Hilden, Germany). The samples were genotyped using the Illumina PorcineSNP60 v2 Genotyping BeadChip containing 64 232 genome-wide SNPs (Ramos et al. 2009). The initial dataset was clustered, called, quality controlled and filtered using GenomeStudio v2.0.0 (Illumina, San Diego, CA, USA). SNPs underwent preliminary clustering using the PorcineSNP60 v2 manifest and low intensity SNPs (mean normalized intensity of the heterozygote cluster < 0.2) were discarded. All SNPs with a cluster separation score < 0.35, high or low heterozygote frequency (> 0.6 or = 0), an excess heterozygote score in relation to the Hardy–Weinberg equilibrium (< -0.3 or > 0.3) or a GenTrain score < 0.7 were evaluated for manual cluster definition and ambiguously clustered or failed SNPs among these were discarded. After manual curation, any SNPs with < 0.95 call frequency were discarded. The final dataset consisted of 56 024 SNPs. Based on the recommendations of Manichaikul et al. (2010), no-based pruning was conducted prior to analysis. In PLINK2 ver. 2.0.0 (Chang et al. 2015), the `-make-king-table` flag was used to estimate pair-wise kinship coefficients following the KING-robust algorithm (Manichaikul et al. 2010). Based on the kinship coefficients, kinship categories were inferred according to thresholds described by Manichaikul et al. (2010). Pairwise kinship coefficients were plotted against the proportion of zero identical-by-state (IBS0) SNPs (Supporting information), to determine a threshold by which to divide 1st degree relatives,

Table 1. Information about seven wild boar dispersers shot in Norway during the years 2019–2021. Kinship coefficients estimated according to KING (Manichaikul et al. 2010) were used to infer kinship and identify the closest relative among another 185 genotyped wild boar sampled across the core distribution range in Norway (N; n=119) and Sweden (S; n=66). ¹Weight reported as carcass weight. ²Weight reported as carcass weight, but only as a rough estimate without weighing. ³4th degree or less related.

ID	Locality shot	Date shot	Weight (kg)	Sex	Dispersal distance (km)	Kin coefficient	Kinship inference of closest relative	Population of closest relative
d1	Stugudal	31.10.2019	65 ¹	male	431	0.010	Unrelated ³	Västmanland (S)
d2	Klæbu	09.11.2019	54 ¹	male	267	0.124	2nd degree	InnlandetN (N)
d3	Midtskogen	01.12.2020	36 ¹	male	81	0.172	2nd degree	InnlandetN (N)
d4	Unset	02.12.2020	38 ¹	male	119	0.114	2nd degree	InnlandetN (N)
d5	Verdal	25.01.2021	50 ²	male	328	0.048	3rd degree	InnlandetN (N)
d6	Nesbyen	31.01.2021	59 ¹	male	323	0.037	Unrelated ³	Dalarna (S)
d7	Sjølisand	13.03.2021	60 ¹	male	61	0.065	3rd degree	InnlandetN (N)

where parent–offspring relations were distinguished from full siblings by an IBS0 < 0.001. We used linear regression to investigate whether pairwise kinship coefficient decreased with pairwise geographic distance.

Dispersal distances were calculated as the distance from each disperser to the nearest individual in the sampling area with the closest relative based on kinship coefficients. These dispersal distances may in reality be somewhat shorter or longer than reported because we only had the center point of the county available for the wild boars from Sweden.

Harvest density reflects variation in population density of wild boar (Augustsson et al. 2024). We calculated density as

mean number of shot wild boar per 10 km² for the hunting years 2018–2022 for hunting management precincts (Sweden) and municipalities (Norway). Swedish data were obtained from Swedish Association for Hunting and Wildlife Management, and in Norway from Statistics Norway.

Results

All seven dispersers were males, and their body weights (mean 51.7 kg) were consistent with younger age classes (Table 1). Kinship inference revealed that the 192 wild boar constituted

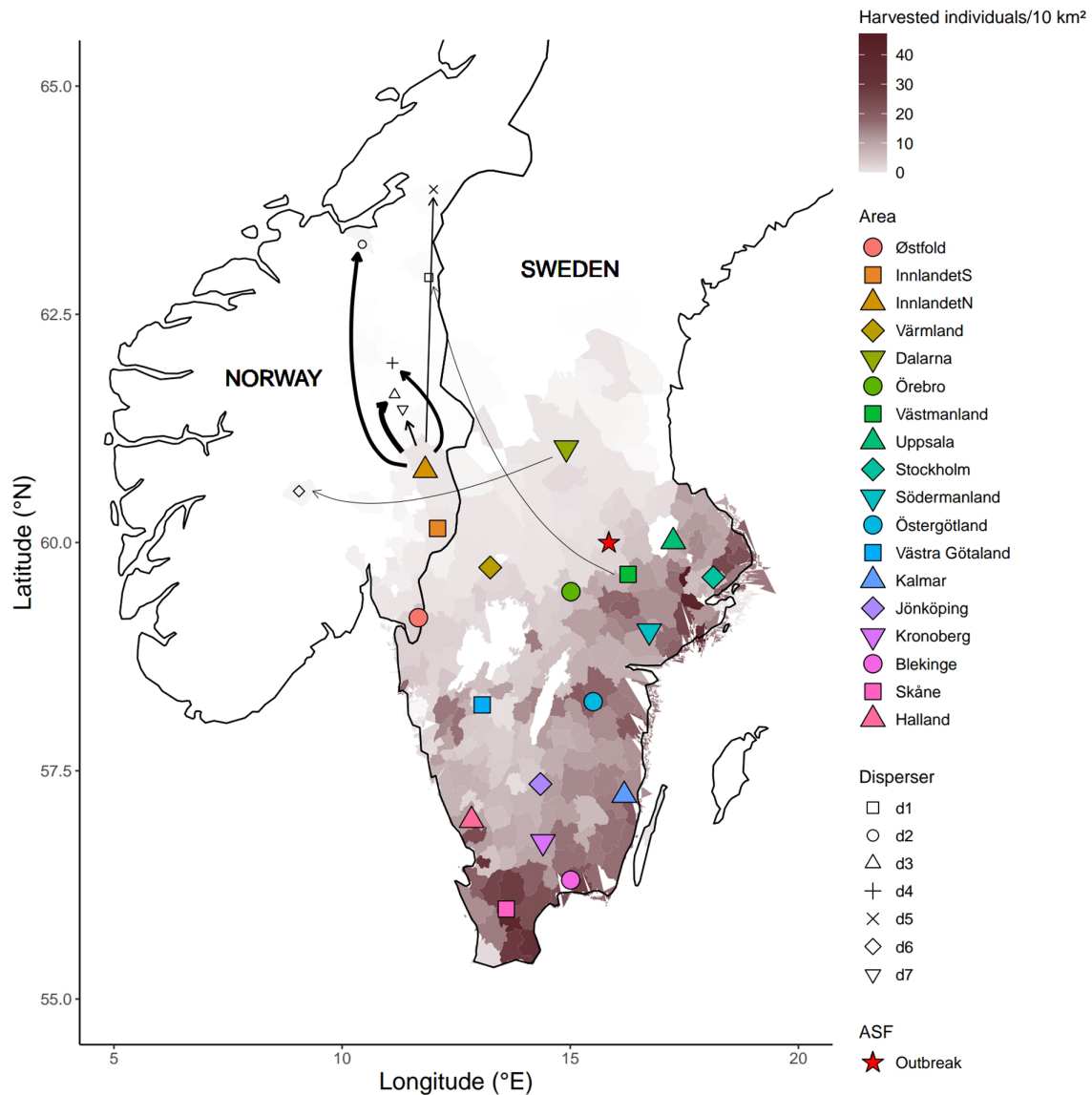


Figure 1. Map with localities where the seven wild boar dispersers (d1–d7) were shot; arrows indicate the sampling area with the closest relative among the other 185 genotyped wild boar. The width of the arrows indicates the kinship coefficients. Wider arrows indicate higher coefficients and likely more closely related individuals. The distribution range and density of wild boar in Norway and Sweden is indicated by the brown background colour, which is the annual number of harvested wild boar per 10 km² during the years 2018–2022 in Norway and Sweden. The red star indicates the area in Sweden where African swine fever was detected, for the first time on the Scandinavian peninsula, in 2023.

a wide range of kin categories, from parent–offspring to unrelated individuals (Supporting information). For five of the seven dispersers, the closest relative was sampled in the range margin in Norway (sampling area InnlandetN, Fig. 1). The final two dispersers had no close (i.e. 3rd degree or closer) relatives among the analysed wild boar. Although they were categorized as unrelated, they were genetically most similar to wild boar from Sweden, one with an individual in Västmanland and the other with an individual in Dalarna. Two of the dispersing individuals (d3 and d4, Table 1) were full siblings as indicated by the kinship inference (kinship coefficient = 0.221). Dispersal distances varied from 61 to 431 km (mean = 230), and the longest estimated distance (431 km) was for one of the dispersers (d1) with the most likely origin in Sweden (Table 1). When all wild boar were considered, the kinship coefficient decreased with pairwise geographic distance (km; Adjusted $R^2 = 0.1556$, slope = -0.0004 , p -value < 0.0001; Supporting information).

Discussion

The current wild boar distribution in Norway mainly reflects a history of persecution. Distribution modelling suggests wild boar could inhabit larger areas mainly along the coast of Norway (VKM et al. 2018), and increased range distribution is expected if no management action is taken. Wild boar form stable matrilineal social groups with a marked spatial genetic structure (Poteaux et al. 2009, Podgórski et al. 2014). The kinship analysis clearly indicated the source population of most long-distance dispersers was the northernmost wild boar distribution area in Norway, hence indicating pre-saturation dispersal. However, all dispersers were males, reducing the probability of reproduction and establishment of new, self-sustaining populations of wild boar in these areas. Body weights were indicative of younger age classes (Table 1), and most of the cases likely represent natal dispersal by juveniles and possibly subadults.

Male-biased juvenile dispersal limits colonization speed (Loe et al. 2009), while high juvenile dispersal rates of both sexes lead to more rapid colonization (Andersen et al. 2004). Despite limited sample size, our detection of male-only long-distance dispersers is consistent with studies from endemic areas. Juvenile dispersal was male-biased in Belgium, averaging 4.9 km in males and 2.5 km in females (Prévot and Licoppe 2013), and female wild boar had shorter dispersal distances (4.5 km) than males (16.6 km) in Sweden (Truvé and Lemel 2003). However, colonization speed is likely lower than average dispersal distances. In Japan, wild boar range expansion was predicted at 2.2 km/year (Saito et al. 2012), and these rates are likely more realistic for range expansion than those derived from dispersal distances.

The Norwegian Food Safety Authority fears the movement of wild boar from Sweden may introduce ASF to Norway (Norwegian Environment Agency and Norwegian Food Safety Authority 2024). Long-distance dispersal is considered to be rare in established populations in Sweden (Truvé and

Lemel 2003), but cases of 300–500 km are reported elsewhere (Jerina et al. 2014, Popczyk et al. 2024). Kinship analysis suggested that one of the Norwegian dispersers had an estimated origin 431 km away, close to the area where an ASF outbreak has been reported in Sweden (Fig. 1). As relatively few wild boar were genotyped in this region, a more comprehensive sampling strategy would be required to pinpoint a more exact origin. Further, wild boar movement was a poor predictor of ASF spread in Poland, due in part to the short duration of clinical period with virus shedding and high and quick virus-induced lethality (Podgórski and Smietanka 2018). Long-distance dispersal of wild boar is not a likely route of ASF dissemination in the current epidemiological situation in Scandinavia. However, dispersal may be relevant for spread of other pathogens with a longer incubation period, and of other propagules like plant seeds (Schmidt et al. 2004).

Our study has implications for wild boar control measures, such as the suggestion to fence the border. The origin of most long-distance dispersers was from Norway, and hence will continue irrespective of border fencing. Individuals living close to the border will nevertheless be a continued threat to spread in the case of future disease outbreak.

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Author contributions

Christer M. Rolandsen: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Project administration (lead); Writing - original draft (supporting); Writing - review and editing (supporting). **Oddmund Kleven:** Conceptualization (equal); Formal analysis (supporting); Investigation (equal); Methodology (lead); Writing - original draft (supporting); Writing - review and editing (supporting). **Lina G. Arntsen:** Formal analysis (lead); Investigation (equal); Writing - original draft (supporting); Writing - review and editing (supporting). **Göran Bergqvist:** Data curation (supporting); Writing - review and editing (supporting). **Marie L. Davey:** Formal analysis (supporting); Writing - review and editing (supporting). **Carl Andreas Grøntvedt:** Investigation (supporting); Writing - review and editing (supporting). **Jonas Kindberg:** Writing - review and editing (supporting). **John Odden:** Writing - review and editing (supporting). **Inger Maren Rivrud:** Writing - review and editing (supporting). **Jørgen Rosvold:** Writing - review and editing (supporting). **Neri Horntvedt Thorsen:** Writing - review and editing (supporting). **Erik Ågren:** Investigation

(equal); Writing - review and editing (supporting). **Atle Mysterud**: Conceptualization (equal); Writing - original draft (lead); Writing - review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.djh9w0w7f> (Rolandsen et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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